Paleontological Research, vol. 3, no. 4, pp. 287–293, 5 Figs., December 30, 1999

Hilgendorf's planorbid tree–the first introduction of Darwin's Theory of Transmutation into palaeontology

HORST JANZ

Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D–70191, Stuttgart, Germany

Received 31 March 1999; Revised manuscript accepted 16 September 1999

Abstract. Franz Hilgendorf (1839–1904)'s palaeontological studies on the Miocene planorbid snails of the Steinheim basin (Germany) frame his scientific work from his dissertation in 1863 to his last publication on this subject in 1901. Hilgendorf discovered that the different planorbids are not mixed in each layer, and noticed gradual transitions between different morphs of successive layers. These findings led to his hypothesis of species transmutation illustrated by his planorbid tree. This was the first phylogenetic tree reconstructed on the basis of real fossil evidence, and therewith it was the first palaeontological example of Darwin's Theory of Transmutation. Although Hilgendorf did not refer to Darwin emphatically, he can be called the first one who introduced Darwin's Theory of Transmutation into palaeontology.

Key words: Hilgendorf, phylogenetic tree, planorbids, Steinheim, theory of transmutation

Introduction

Franz Hilgendorf is famous mainly for his zoological work, of which the Hilgendorf Exhibition (Yajima, 1997, 1998) focused on his merits for ichthyology and fishery sciences in Japan. However, his palaeontological work is no less important. Hilgendorf started his scientific career with a palaeontological study on the Miocene planorbid snails of the Steinheim basin. This was the subject of his dissertation (Hilgendorf, 1863) and of his first publication (Hilgendorf, 1866), and although he was later on mainly concerned with zoological subjects, the Steinheim snails remained on his mind for the rest of his life. His last paper on the Steinheim snails was published three years before his death (Hilgendorf, 1901). Thus, the planorbid studies frame his scientific work.

Already in his first study Hilgendorf recognised gradual transitions between the snails of successive layers. He documented and interpreted these findings in his first publication with a phylogenetic tree, which is the first palaeontological documentation of species transmutation. His hypothesis, heavily disputed at that time, was largely confirmed over the last two decades (Mensink, 1984; Gorthner, 1992; Povel, 1993; Nützel and Bandel, 1993; Finger, 1998).

Although Hilgendorf's findings were most important for the discussion of Darwin's Theory, which was published only few years before (Darwin, 1859), Hilgendorf did not refer emphatically to Darwin in his papers. On the other hand, Darwin himself mentioned Hilgendorf in his sixth edition of the 'On the origin of species..', published in 1872, within Chapter 10 (On the imperfection of the geological record), subchapter 'On the absence of numerous intermediate varieties in any single formation', as follows: "... Hilgendorf has described a most curious case of ten graduated forms of *Planorbis multiformis* in the successive beds of a fresh-water formation in Switzerland" [wrong geographic information by Darwin]. Hilgendorf's historical role has been already recognised by Abel (1929), and the significance of Hilgendorf's studies from a Neo-Darwinian point of view is discussed in detail by Reif (1983a, 1983b, 1985, 1986).

To assess whether Hilgendorf was familiar with Darwin's Theory, the present paper gives a brief chronological survey of Hilgendorf's planorbid studies, paying special attention to remarks on Darwin and Darwinism. Finally, a brief account of the research on the Steinheim snails after Hilgendorf's death with emphasis on the connection between Hilgendorf's contribution and the latest work at Steinheim is added. Before that, some information about the Steinheim basin, and also the state of knowledge of the Steinheim snails before Hilgendorf are given.

The Steinheim basin–a meteorite crater

The Steinheim basin is situated on the Swabian Alb in southern Germany (Figure 1). Today it is known that the basin was formed by a meteorite impact, about 15 million years ago, which is, expressed in geological time, the Middle Miocene of the Tertiary. The Steinheim basin is a complex impact crater structure with an almost circular outline, and a central uplift, called the central hill. The basin has a diameter of about 3.5 km, and is 120 m deep today. Soon after the impact the crater filled with water and became a lake. It is supposed that the water supply came mainly from the subterranean karst system and from precipitation. How

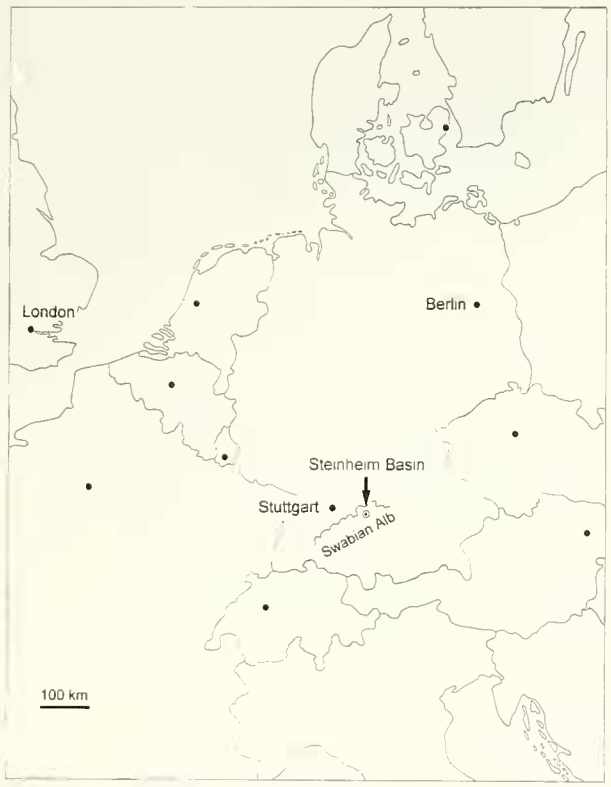

Figure 1. Location of the Steinheim basin.

long the lake actually existed is not exactly known. Between some hundreds of thousands to two million years are suggested. This is what we today call a long-lived lake (Gorthner, 1994). At the end of the lake period the basin was completely filled with lake sediments. The fact that we can recognise the basin again today is due to partial erosion during the Quaternary, the last two million years. However, the lake sediments preserved reach a thickness of 30 to 40 meters, and are very rich in well preserved fossils. About 100 species of fossil plants and more than 250 species of fossil animals have been found so far. The snails comprise about 100 species, of which the planorbids are the most abundant group.

The knowledge of the Steinheim snails before Hilgendorf

In 1862 when Hilgendorf started his studies not much was known about the Steinheim basin, neither about its origin nor its palaeontology. However, the occurrence of amazing quantities of calcareous shells within the Steinheim sands was documented for the first time already about 150 years before, by the physician Lentilius (1711). Lentilius was fascinated by the amount and multiformity of these shells, and it seemed to him enigmatic for what reason God had created such a variety of tiny shells (Figure 2). At that time it was not yet known that these shells are remains of once living animals, what we call today fossils, but it was believed that all species were created by God and remained unchanged since their creation. This dogma of the fixity of species was still universal when the study of von Klein (1847) was publi-

Figure 2. Ensemble of Steinheim snails within the sediment (photo: H. Lumpe, Staatliches Museum für Naturkunde Stuttgart). The width of the shells is about 4 to 5 mm.

shed. Von Klein's study is one of the first scientific studies of the Steinheim snails and reflects the latest knowledge about this subject at the time when Hilgendorf started with his studies. Von Klein distinguished five planorbid species, four of which he allocated to the genus *Planorbis*, and one to the genus *Valvata*. From the latter species, called *Valvata multiformis*, he distinguished five varieties. According to von Klein all of these species and varieties occurred always mixed within each layer of the Steinheim deposits.

Hilgendorf's dissertation and first publication

Before Hilgendorf went to Tübingen he had studied in Berlin for two years. He came to Tübingen in 1862, attracted by Friedrich August Quenstedt, in order to study palaeontology. Quenstedt was a professor of geology and palaeontology at the University of Tübingen, and became famous by his comprehensive stratigraphical investigations of the Jurassic Swabian Alb by means of ammonites. In the autumn of 1862, Hilgendorf accompanied Quenstedt on an excursion to Steinheim, during which he first became acquainted with the Steinheim basin and its snails.

By collecting snails in Pharion's sand pit on this excursion, as well as during the following weeks, Hilgendorf discovered that the different varieties of *Valvata multiformis* are never mixed, but that they occur separately in the different layers. From the lowermost beds onwards he noticed a sequence of flat or planispiral shells to trochispiral shells and again to planispiral ones in the upper parts of the section. Moreover, the different morphs were connected by transitional morphs. Most surprising was the discovery that transitions were not only found between the different varieties of *Valvata multiformis* but also between species of *Planorbis* and some of the varieties of *Valvata* – in other words: he found gradual transitions between two different genera. These findings, of course, were not compatible with the dogma of the fixity of species.

Hilgendorf stated these findings in his dissertation which was submitted in spring, 1863. His dissertation comprises 42 pages, and does not include any figures. In the 1980s Prof. Wolf-Ernst Reif from the Palaeontological Institute of the University of Tübingen discovered a collection of 25 cards of thick paper with Steinheim snails glued onto it which could be clearly identified as Hilgendorf's, because of hand-written captions on the cards (Reif, 1983a).

While each of the cards from no. 1 to no. 17 contains snails of different beds, the cards no. 18 to no. 25 illustrate transitions from one taxon to another, and card no. 24 gives a complete phylogenetic diagram of Hilgendorf's results. Reif (1983a) reconstructed a phylogenetic diagram according to card no. 24 (Figure 3). It corresponds fairly well with Hilgendorf's interpretation given in his dissertation, and shows three modes of species transformation in course of time: 1. gradual transformation, 2. splitting into two daughter species, and 3. fusion of two species.

Actually, Hilgendorf never seriously suggested fusion of lineages, but merely raised it as a doubtful possibility. Considering the planorbid varieties of the third layer (see Figure 3, layer D), he raises the question of whether fusion of

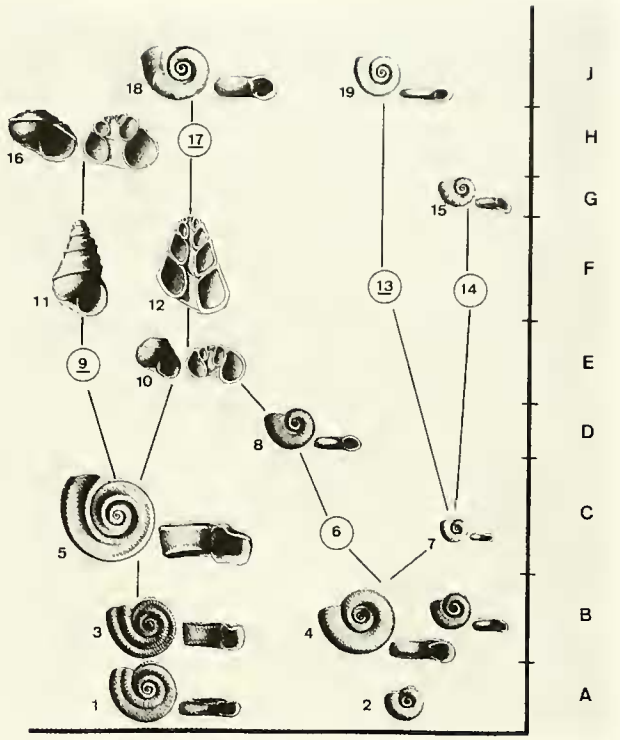

Figure 3. Reconstructed phylogenetic diagram of Hilgendorf's dissertation according to card no. 24. Circled numbers: either not identifiable (underlined) or missing. Examples for species transformation are: 1. gradual transformation: sequence from no. 1 to no. 5; 2. splitting into two daughter species: no. 5 splits into no. 9 and no. 10; 3. fusion of two species: no. 8 and no. 10. Reproduced from Reif (1983a, fig. 3) with permission of Paläontologische Gesellschaft.

two varieties could have led to this situation (Hilgendorf, 1863, p. 26). However, on the last page of his dissertation, there is an additional note to this subject (Hilgendorf, 1863, p. 42): "Darauf würde das schöne Bild, das Darwin uns vom Zusammenhange der Spezies in einem Zweige-reichen Baume vorführt, nicht passen, die Zweige eines Baumes wachsen nicht wieder zusammen." [This does not fit the nice picture of a tree with many branches which Darwin presented to illustrate the descent of the species – the branches of a tree never fuse again]. This note also exemplifies that Hilgendorf was already acquainted with Darwin's Theory during his first study.

Already after one year at Tübingen Hilgendorf went back to Berlin and continued his studies of natural sciences, especially organic chemistry, but subsequently he concentrated more and more on zoology. He got a position at the Humboldt Museum, and in 1865 he again started an investigation of the Steinheim snails, which was supported by the Royal Prussian Academy of Sciences. This new field work at Steinheim took two months and led to his first publication (Hilgendorf, 1866), which is still today the crucial publication on the Steinheim snails.

This paper is based on a study of a large amount of

material collected thoroughly bed by bed from three sand pits around the central hill, as well as from the western margin of the basin. Already the title of this paper: "*Planorbis multiformis* im Steinheimer Süsswasserkalk" [*Planorbis multiformis* within the calcareous freshwater deposits of Steinheim], reveals Hilgendorf's solution of the taxonomic problems, which confronted him through his findings. He considered all planorbid snails found to belong to one species, *P. multiformis*. And the subtitle: "Ein Beispiel von Gestaltveränderung im Laufe der Zeit" [An example of morphological change during time], so to say, gives an explanation for his solution. Moreover, this is also a clear confession of belief in Darwin's Theory of Transmutation.

However, Hilgendorf did not refer to Darwin in this paper. The first part of the publication comprises a detailed stratigraphical description of the sections, and a morphological characterisation of the 19 varieties or subspecies of *P. multiformis* which he distinguished. Using the biostratigraphical distribution of these subspecies, Hilgendorf subdivided the Steinheim deposits into ten zones or beds. In the second part of the paper he discussed the transitions between subspecies of successive beds. By arranging the subspecies in a stratigraphical scheme and marking transitions between two subspecies by a connecting line, Hilgendorf's phylogenetic tree became graphical. The planorbid tree is illustrated in the middle of the lithographic plate at the end of the paper, surrounded with illustrations of all subspecies, including also cross-sections of the snails.

Figure 4 shows a reconstructed and magnified version of this tree. The whole tree arises from a small and planispiral planorbid, called *aequeumbilicatus*, which is considered the founder population. The branch at the right hand comprises ten bigger morphs. Today, this branch is called the 'main branch', and is the most studied and discussed part of the tree so far. Especially the transition between the trochispiral form *trochiformis* and the planispiral form *oxystommus* later became a subject of controversial discussions. While the second branch, in the middle of the tree, splits from the *steinheimensis* form, and comprises only two forms, the third branch, at the left hand, splits from the founder population, and comprises seven forms. Today, these two branches are called the 'side branches'.

In contrast to the diagram reconstructed by Reif (1983a), according to Hilgendorf's cards and dissertation, this new tree involves only two modes of speciation: gradual transformation and splitting, but no fusion. Additionally, the whole tree arises from one founder species. This interpretation was compatible with Darwin's Theory.

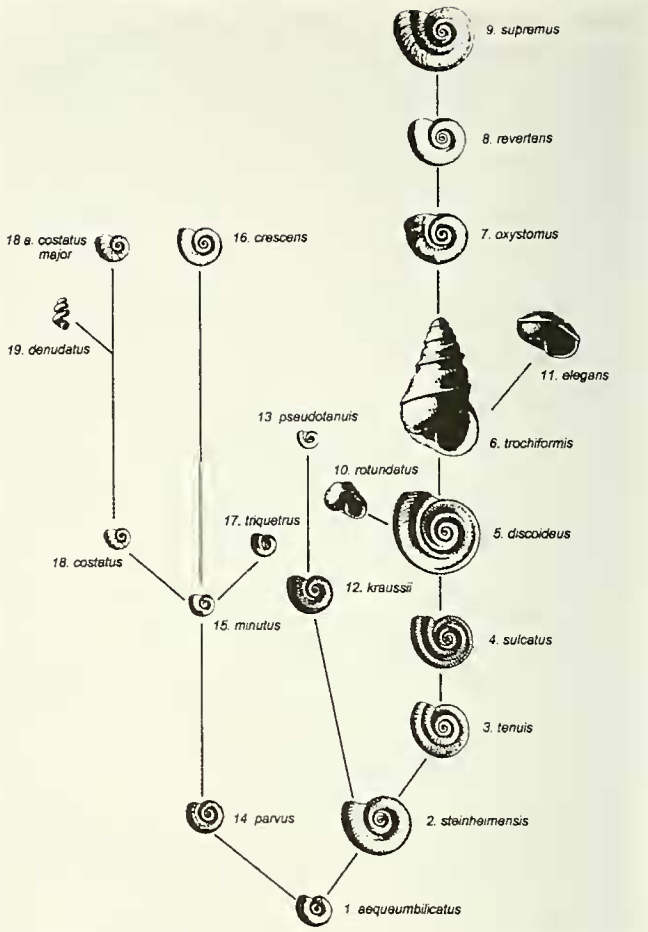

Figure 4. Reconstructed version of Hilgendorf's 1866 planorbid tree.

The controversy with Sandberger

There was no critical reaction to Hilgendorf's publication for the first few years, but during the time Hilgendorf was in Japan, Fridolin von Sandberger started to controvert Hilgendorf. Sandberger was a professor of geology at Würzburg, and he was reputed to be an authority on fossil snails. By three very short articles (Sandberger, 1873, 1874a, 1874b), he totally rejected Hilgendorf's interpretation. Sandberger neither accepted the allocation of all Steinheim planorbids to one species, nor the occurrence of the different varieties of *Valvata* in a stratigraphically orderly fashion, nor the transitions, but sustained von Klein's concept, and thus the fixity of species.

Hilgendorf got wind of Sandberger's criticism in Tokyo, and commented on it in November 1874, with a letter to his friend Eduard von Martens, which was published in the "Zeitschrift der Deutschen Geologischen Gesellschaft" (Hilgendorf, 1875). The controversy lasted till 1877 and reached its summit at the 'Meeting of Natural Scientists and Physicians' in Munich. Although the dispute exemplifies Hilgendorf's excellent attitude of being always obliged to the facts, I do not want to discuss it in detail (see Hilgendorf 1877a, 1877b, 1877c, 1877d). Summarising, the following assessment can be given:

1. The background of Sandberger's attacks had been only to a minor extent a dispute against the validity of Darwin's Theory. Unfortunately, the dominant motivation for his rigid attitude apparently was his antipathy toward the Prussians (see Hilgendorf, 1879, p. 90).

2. However, responding to Sandberger's accusation, Hilgendorf had checked his findings again and again by field

investigations, and had found more evidence of his hypothesis.

3. Despite the trouble that Hilgendorf had to suffer from this controversy, another positive effect was that his findings became well known in professional circles, and finally most of the experts accepted his hypothesis.

In order to demonstrate the stratification, as well as the transitions, at the Munich Meeting, Hilgendorf had collected new material and had taken photographs during his third season of field activities in Steinheim, which took nine weeks. One of these photos, actually assembled from two photos, is a panoramic view of the western side of the central hill. At that time, the sand pit had still a large expanse. Another photo taken by Hilgendorf himself shows a detail of Pharion's sand pit, obviously taken to demonstrate the stratification, because it shows the same part of Pharion's sand pit as a sketch drawn by Hilgendorf.

Hilgendorf's planorbid papers after 1877

Concerning Hilgendorf's familiarity with Darwin's Theory, his publication of 1879 (Hilgendorf, 1879) provides most clear evidence. This paper was published in the journal "Kosmos" which was founded only two years before, in 1877, for the purpose of promoting the concept of natural evolution. On the editorial board appear the names of Charles Darwin and Ernst Haeckel. Haeckel was the most prominent exponent of Darwinism in Germany, and had coined the term "Phylogenie" in 1866.

Hilgendorf (1879) gives a full account of his data and his theoretical concepts. The paper contains a newly drawn phylogenetic tree, showing most of the snails in cross-sections (Figure 5). The tree is almost identical with that of 1866, except that the founder population is missing. Already in 1866 Hilgendorf was in doubt whether there was only one planorbid form in the lowermost beds from which all the other forms had been developed. Now he withdrew this hypothesis, because it seemed to him that too little was known about the deposits on the western margin of the basin where this form occurs. In this paper Hilgendorf also formulated a concept for the recognition of evolutionary lineages in palaeontology including the practical method of bed-by-bed investigation. Finally, he summarised his data and his interpretations in 27 theorems. These theorems also contain problems and hypotheses, which became a subject of discussion only later, for example the law of irreversibility of evolutionary changes. Nevertheless, Hilgendorf did not speculate on the reasons for the species transmutation in the Steinheim basin. This seemed to him still too early, but he gave some hints for further investigations, for example to check the embryonic part of the gastropod shells, which should provide evidence for speciation, and to check other groups of Steinheim fossils for transmutation (Hilgendorf, 1879, p. 94 and 98). Hilgendorf mentioned in his paper of 1879 also the findings of Neumayr and Paul (1875) who had also found gradual transformations in Tertiary gastropods of Slovenia. In a footnote of their paper they credited Hilgendorf as the first one who had provided evidence for gradual transformation by a detailed palaeontological study.

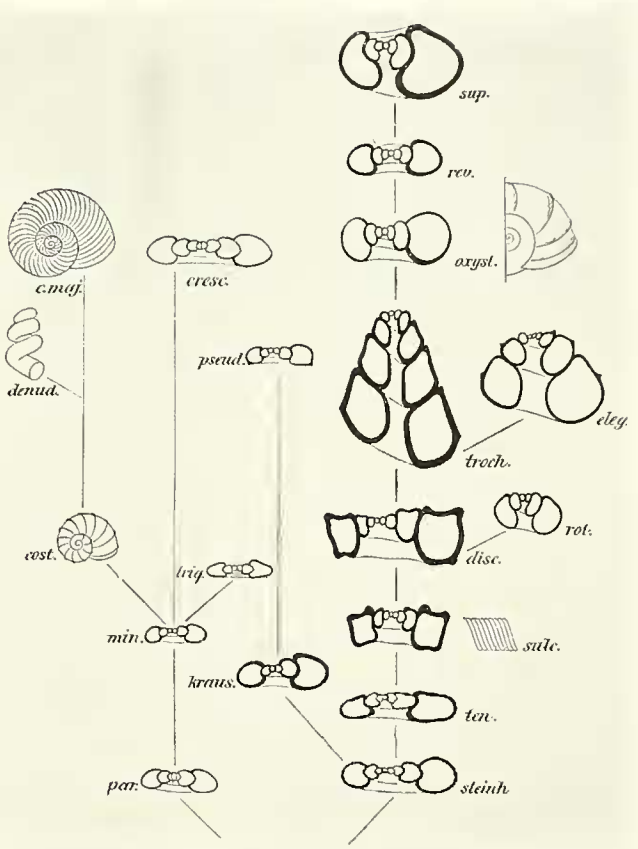

Figure 5. Planorbid tree of Hilgendorf (1879). Reproduced with permission of *Kosmos*.

After 1879, two additional papers of Hilgendorf (1881, 1901) on the Steinheim snails were published. In 1881 he commented on the paper of Hyatt (1880). Hyatt was an American scientist, who had been studying the Steinheim snails since 1872. Then, Sandberger had claimed that Hyatt's view would support his statements and would disprove Hilgendorf's interpretation. But in fact, Hyatt was a Darwinian, and was attracted to this study by Hilgendorf's first publication. Generally speaking, Hyatt's findings support Hilgendorf's interpretation, except for some differences in the question of the stem species and the transition between the trochispiral and the planispiral form. Moreover, Hyatt promoted Hilgendorf's subspecies to species rank.

In his last paper Hilgendorf (1901) once again took care of the most disputed transition between the trochispiral and the planispiral form, and illustrated the transitions by a series of photographs.

The planorbid tree after Hilgendorf's death

From 1901 to the present day more than 30 papers on the Steinheim planorbids have been published. Till the beginning of the last decade the most important steps confirming Hilgendorf's findings were made by Gottschick (1920) and Wenz (1922), as well as Mensink (1984). Gottschick and Wenz have been the first who examined again the Steinheim

snails of all beds in detail. Although, in contrast to Hilgendorf, they regarded the morphological changes of the planorbids as ecophenotypic, they fully confirmed the occurrence of the different morphs within the different beds. Mensink also studied the planorbids of all beds, and additionally he checked the occurrence of Hilgendorf's main branch planorbids at a large number of sites spread over the whole Steinheim basin. Moreover, Mensink demonstrated the gradual transitions of the main branch planorbids by means of biometrical investigations. The significance of Gottschick's and Mensink's results are discussed in detail by Reif (1985), and recently, Mensink's data set was reconsidered by means of multivariate methods (Povel, 1993).

In connection with Hilgendorf's (1879) hints for further investigations mentioned above, *i.*e., to study the embryonic part of the shells and to check other groups of Steinheim fossils, both approaches were carried out only during the last decade, more than 100 years after Hilgendorf's publication. With respect to the embryonic part of the gastropod shells (protoconch), Gorthner (1992) and Nützel and Bandel (1993) were able to show by means of SEM analyses of the protoconch structures that both Hilgendorf's main branch and side branch planorbids are valid species. Moreover, the most recent study shows by such protoconch analyses that Hilgendorf's *aequeumbilicatus*, which is called *Gyraulus kleini* today, did not consist of three different species giving rise to three lineages as Gottschick (1920) suggested, but that *Gyraulus kleini* was the only founder species of the whole planorbid lineage (Finger, 1998).

Hilgendorf's second hint, to check other Steinheim fossils for morphological changes, was taken up in a detailed bed-by-bed study of the Steinheim ostracods (Janz, 1992, 1997). Ostracod shells are the most abundant fossils among the Steinheim deposits, and there are also some species which show morphological changes through the profile. In the genus *Leucocythere*, speciation by a splitting event was detected (Janz, 1992), and the splitting hypothesis could be supported by a detailed study of the microfeatures of *Leucocythere* shells by Viehofen (1997). Moreover, the ostracod assemblage shows a pattern of shell alteration through the profile similar to that of the planorbids (Janz, 1993, Janz, in press). As to the reasons for these alterations, on which Hilgendorf did not speculate, there are two major factors possibly provoking evolutionary changes in both snails and ostracods: long-term ecological changes, as well as the longevity of the lake. While the long-term ecological changes were mainly due to lake level fluctuations, the longevity of the former Lake Steinheim was postulated by Gorthner and Meier-Brook (1985) because of the similarity of the heavily sculptured planorbids with endemic species of extant ancient lakes.

Conclusions

Summing up this brief chronological survey of Hilgendorf's studies on the Steinheim snails, it can be concluded:

1. By looking at Hilgendorf's palaeontological work more closely, it becomes evident that Hilgendorf was already a convinced Darwinian from the beginning of his studies.

2. Hilgendorf set a high value on demonstrating the objectivity of his methods of working based on an inductive approach, and perhaps for this reason did not refer to Darwin in his papers.

3. Nevertheless, he applied Darwin's Theory of Transmutation by his interpretation of the Steinheim snails, and therefore he can be called the first one to introduce Darwin's Theory into palaeontology.

4. Hilgendorf's interpretation has been generally confirmed by further studies, and hints he had given have led to findings supporting his hypothesis. However, there are still many questions to be answered, in order to fully understand the Steinheim planorbid tree.

Acknowledgements

I am much indebted to Michiko Yajima for stimulating me to write this paper by organising an exhibition as well as a symposium on Franz Hilgendorf in Japan. I also thank her very much for her continuous interest and helpfulness. The two referees, Wolf-Ernst Reif and Roger D. K. Thomas, are acknowledged for their useful comments and suggestions which certainly improved this paper.

References

Abel, O., 1929: *Paläobiologie und Stammesgeschichte*. 423 p. G. Fischer, Jena.

Darwin, C., 1859: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 502 p. J. Murray, London.

Finger, I., 1998: Gastropoden der *kleini*-Schichten des Steinheimer Beckens (Miozän, Süddeutschland). *Stuttgarter Beiträge zur Naturkunde, ser. B*, no. 259, p. 1-51.

Gorthner, A., 1992: Bau, Funktion und Evolution komplexer Gastropodenschalen in Langzeit-Seen. Mit einem Beitrag zur Paläobiologie von *Gyraulus "multiformis"* im Steinheimer Becken. *Stuttgarter Beiträge zur Naturkunde, ser. B*, no. 190, p. 1-173.

Gorthner, A., 1994: What is an ancient lake? *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie*, vol. 44, p. 97-100.

Gorthner, A. and C. Meier-Brook, 1985. The Steinheim Basin as paleo-ancient lake. *In*, Bayer, U. and Seilacher, A. *eds., Sedimentary and Evolutionary Cycles. Lecture Notes in Earth Sciences 1*, p. 322-334. Springer, Berlin, Heidelberg, New York and Tokyo.

Gottschick, F., 1920. Die Umbildung der Süßwasserschnecken des Tertiärbeckens von Steinheim a.A. unter dem Einflusse heißer Quellen. *Jenaische Zeitschrift für Naturwissenschaft*, vol. 56 (New series 49), p. 155-216.

Hilgendorf, F., 1863: *Beiträge zur Kenntniß des Süßwasserkalkes von Steinheim*, 42 p. Dissertation for University of Tübingen.

Hilgendorf, F., 1866: Planorbis multiformis *im Steinheimer Süßwasserkalk. Ein Beispiel von Gestaltveränderung im Laufe der Zeit*, 36 p. Buchhandlung von W. Weber, Berlin.

Hilgendorf, F., 1875: Briefliche Mitteilungen. Herr F. Hil-

gendorf an Herrn E. von Martens. *Zeitschrift der Deutschen Geologischen Gesellschaft*, vol. 27, p. 224–227.

Hilgendorf, F., 1877a: Noch einmal *Planorbis multiformis*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, vol. 29, p. 50–62.

Hilgendorf, F., 1877b: Neue Forschungen in Steinheim. *Zeitschrift der Deutschen Geologischen Gesellschaft*, vol. 29, p. 448–456.

Hilgendorf, F., 1877c: Neue Untersuchungen über *Planorbis multiformis*. *Münchener Versammlung der Naturforscher und Ärzte, 1877*, p. 156–157.

Hilgendorf, F., 1877d: Die Streitfrage des *Planorbis multiformis* betreffend. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1877*, p. 268–269.

Hilgendorf, F., 1879: Zur Streitfrage des *Planorbis multiformis*. *Kosmos*, vol. 5, p. 10–22, 90–99.

Hilgendorf, F., 1881: Die neu erschienene Schrift "The genesis of the tertiary species of *Planorbis* at Steinheim" by A. Hyatt. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 1881, p. 95–100.

Hilgendorf, F., 1901: Der Uebergang des *Planorbis multiformis trochiformis* zum *Planorbis multiformis oxystomus*. *Archiv für Naturgeschichte* vol. 67, p. 331–346.

Hyatt, A., 1880: The Genesis of the Tertiary Species of *Planorbis* at Steinheim. *Anniversary Memoir of Boston Society of Natural History*, 1880, p. 1–114.

Janz, H., 1992. Die miozänen Süßwasserostrakoden des Steinheimer Beckens (Schwäbische Alb, Süddeutschland). *Stuttgarter Beiträge zur Naturkunde, ser. B*, no. 183, p. 1–117.

Janz, H., 1993: Die Bedeutung der Ostrakoden (Crustacea) des Steinheimer Beckens für die Diskussion um die Gestaltveränderungen der Planorbidae (Gastropoda) im Laufe der Seegeschichte. *Jahreshefte der Gesellschaft für Naturkunde Württemberg* no. 148, p. 33–51.

Janz, H., 1997. Die Ostrakoden der *kleini*-Schichten des miozänen Kratersees von Steinheim am Albuch (Süddeutschland). *Stuttgarter Beiträge zur Naturkunde, ser. B*, no. 251, p. 1–101.

Janz, H., (in press). An example of intralacustrine evolution at an early stage: the freshwater ostracods of the Miocene crater lake of Steinheim (Germany). *Hydrobiologia*.

Klein, A. von, 1847: Conchylien der Süsswasserkalkformationen Württembergs. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 2, p. 60–116.

Lentilius, R., 1711: Eteodromus medico-practicus Anni MDCCIX. –XXIV+1362+54 p. Impensis Augusti Mezleri, Stuttgardiae.

Mensink, H., 1984: Die Entwicklung der Gastropoden im miozänen See des Steinheimer Beckens (Süddeutschland). *Palaeontographica A*, no. 183, p. 1–63.

Neumayr, M. and Paul, C., 1875: Die Congerien- und Paludinenschichten Slavoniens und deren Faunen. *Abhandlungen der kais.-koenig. Geologischen Reichsanstalt*, vol. 7, p. 1–111.

Nützel, A. and Bandel, K., 1993: Studies on the side-branch planorbids (Mollusca, Gastropoda) of the Miocene crater lake of Steinheim am Albuch (southern Germany). *Scripta Geologica, Special Issue* 2, p. 313–357.

Povel, G. D. E., 1993: The main branch of Miocene *Gyraulus* (Gastropoda; Planorbidae) of Steinheim (southern Germany): a reconsideration of Mensink's data set. *Scripta Geologica, Special Issue* 2, p. 371–386.

Reif, W.-E., 1983a: Hilgendorf's (1863) dissertation on the Steinheim planorbids (Gastropoda; Miocene): The development of a phylogenetic research program for Paleontology. *Paläontologische Zeitschrift*, no. 57, p. 7–20.

Reif, W.-E., 1983b: The Steinheim snails (Miocene; Schwäbische Alb) from a Neo-Darwinian point of view: A discussion. *Paläontologische Zeitschrift*, no. 57, p. 21–26.

Reif, W.-E., 1985: Endemic Evolution of *Gyraulus kleini* in the Steinheim Basin (Planorbid Snails, Miocene, Southern Germany). *In*, Bayer, U. and Seilacher, A. *eds.*, *Sedimentary and Evolutionary Cycles*, p. 256–295. Springer, Berlin.

Reif, W.-E., 1986. The search for a macroevolutionary theory in German paleontology. *Journal of History of Biology*, vol. 19, no. 1, p. 79–130.

Sandberger, C. L. F., 1873: Uebergänge der Formen der Steinheimer *Planorbis*. *Tageblatt 46, Versammlung der Deutschen Naturforscher und Aerzte Wiesbaden*, p. 130.

Sandberger, C. L. F., 1874a: Die Steinheimer Planorbiden. *Verhandlungen der Physikalisch-Medizinischen Gesellschaft zu Würzburg NF, 5*, p. 231–232.

Sandberger, C. L. F., 1874b: Die Steinheimer Planorbiden. *Jahrbuch der Deutschen Malakozoologischen Gesellschaft*, vol. 1, p. 54–56.

Viehofen, A., 1997: Entwicklung der *Limnocythere*-Arten im Miozän des Steinheimer Beckens, Süddeutschland. *Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln*, vol. 108, 311 p.

Wenz, W., 1922. Die Entwicklungsgeschichte der Steinheimer Planorben und ihre Bedeutung für die Deszendenzlehre. *Berichte der Senckenbergischen Naturforschenden Gesellschaft*, vol. 52, p. 135–158.

Yajima, M. *ed.*, 1997: *Franz Hilgendorf-the Father of Japanese Ichthyology and Fishery Sciences*, 72 p. The Committee of the Hilgendorf Exhibition, Tokyo. (*in Japanese with English title*)

Yajima, M., 1998: Reviews of the Hilgendorf Exhibition. A trial of the travelling exhibition. *Journal of Geography* vol. 107, p. 872–878. (*in Japanese with English abstract*)